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THE ABNORMAL PRESENCE OF TWO OVARIES IN A *CANTHON CYANELLUS CYANELLUS* LECONTE FEMALE (COLEOPTERA: SCARABAEIDAE: SCARABAEINAE)

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Abstract.—The presence of one left ovary with one ovariole and a sole oviduct are anatomical features characteristic of female dung beetles of the subfamily Scarabaeinae. Abnormalities in reproductive system anatomy are quite rare in this subfamily; however, a mature *Canthon cyanellus cyanellus* female was discovered to have two ovaries with one ovariole each and two lateral oviducts. Both ovaries and oviducts were functional. This is the third abnormal female observed since 1930.

Resumen.—La presencia solamente del ovario izquierdo con una ovariola y un oviducto único, son características anatómicas propias de las hembras de los escarabajos estercoleros de la subfamilia Scarabaeinae. Las anormalidades en la anatomía del aparato reproductor en las hembras de esta subfamilia son muy poco frecuentes. Una hembra madura de *Canthon cyanellus cyanellus* presentó dos ovarios con una ovariola cada uno y dos oviductos laterales. Tanto los ovarios como los oviductos eran funcionales. Esta es la tercera de la hembras anormales observadas de 1930 a la fecha.

Key Words: *Canthon cyanellus cyanellus*, Scarabaeinae, ovaries, ovarioles, oviducts

The presence of a single left ovary, ovariole and oviduct is one of the most characteristic aspects of female dung beetle anatomy. This extreme reduction to one ovary and ovariole has been linked with a very low fertility rate and the elaborate and complex nesting behavior exhibited by this group (Halffter and Matthews 1966, Halffter and Edmonds 1982).

The first observations of the presence of a sole ovary and ovariole were done on various undetermined species of Coprini by Roussel (1860). Later, this characteristic was also observed in *Scarabaeus sacer* L., *Scarabeus semipunctatus* F., *Scarabeus variolosus* F., *Scarabeus laticollis* L., *Canthon rutilans* Cast., *Sisyphus schafferi* (L.), *Dichotomius anaglypticus* (Mannerhelm) (sub *Pinotus*), *Copris hispanus* (L.) (Heymons 1929, 1930), *Onthophagus fracticornis* (Preyssler), *Onthophagus nuchicornis* (L.), and *Copris lunaris* (L.) (Willimzik 1930). Observations of a greater number of species have shown that this anatomical characteristic is unique to all females of the subfamily (Robertson 1961, Halffter and Matthews 1966, Ritcher and Baker 1974, Halffter and Edmonds 1982).

Up until now, only two exceptional cases have been described. Heymons (1930) studied an adult *Scarabaeus sacer* L. female with a left ovary containing two ovarioles; Pluot (1979) reported an immature *Onthophagus lecontei* Harold adult female with

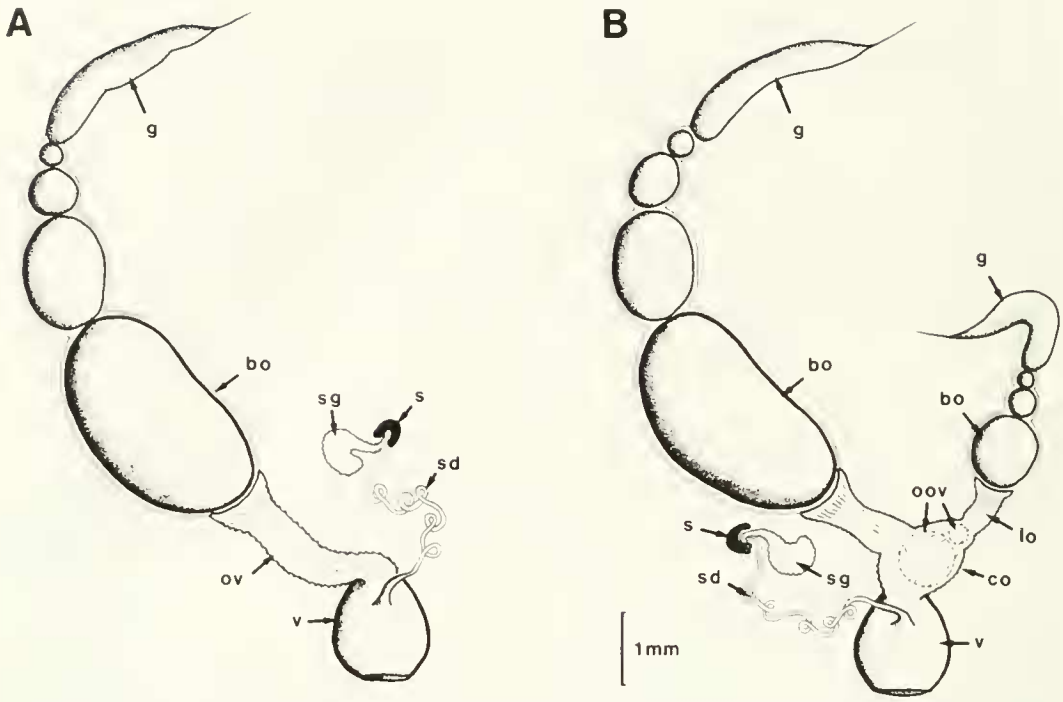

Fig. 1. Schematic drawings of the female reproductive system of *Canthon cyanellus cyanellus* made using a camera lucida. A, Normal. B, Abnormal. Abbreviations: bo = basal oocyte; co = common oviduct; g = germarium; lo = lateral oviduct; oov = oocytes in oviduct; ov = oviduct; s = spermatheca; sd = spermathecal duct, sg = spermathecal gland; v = vagina.

the same anomalies. This study presents a description of the reproductive system of a mature *Canthon cyanellus cyanellus* LeConte female, a necrophagous dung roller beetle from the tropical zone of Veracruz (Mexico), that had two ovaries with one ovariole each and two lateral oviducts.

Material and Methods

The subject of this study came from the brood of *Canthon cyanellus cyanellus* obtained from samples collected in June of 1996 in Los Tuxtlas, Veracruz, Mexico. The brood was kept in controlled environmental conditions (temperature of 27° C, relative humidity of 70%, 14 hour photoperiod, and continual feeding on beef).

The female studied was in a terrarium with a male from the time of emergence. They remained together under the above-mentioned environmental conditions, and she was dissected two and a half months after emergence. The reproductive system was obtained in Ringer saline solution and drawn using the camera lucida. Afterwards, the specimen was fixed in AFATD liquid (alcohol-formol-trichloracetic acid-dimethyl sulfoxide) and was imbedded in Histosec® paraffin. The 8 μm histological cuts were dyed with PAS-Hematoxiline (Gabe 1968).

Results

The reproductive system of the Scarabaeinae female is normally comprised of a left ovary with a single ovariole and oviduct, vagina and spermatheca with its spermathecal gland and duct (Fig. 1A). In the abnormal *Canthon cyanellus cyanellus* female that we describe herein, two ovaries with an ovariole each were present, along with two lateral oviducts, a common oviduct, vagina and spermatheca with its gland and duct (Fig. 1B).

The two ovaries had a well-developed, active germarium similar in size. Both germaria contained active prefollicular cells, trophocytes, and interstitial cells (Fig. 2A, B) and previtellogenic oocytes in the basal region (Fig. 2C, D). Both ovaries had a normal pedicel (Fig. 2E).

The vitellarium of the left ovary contained 4 oocytes. The basal oocyte, a little over 3.5 mm in length, was mature, with a well-formed chorion; it was ready to be ovulated. The three oocytes that followed were of various sizes and were undergoing vitellogenesis. The right ovary had 3 oocytes in vitellogenesis; the basal oocyte measured only 1 mm (Fig. 1B). The follicular epithelium was normal.

The two lateral oviducts appeared to be normal, and both connected to the common oviduct (Fig. 1B). The histological structure of the two lateral oviducts was similar: the wall, quite pleated lengthwise, had an epithelium—of mesodermic origin—covered by a muscular layer (Fig. 2F). The common oviduct, also pleated lengthwise, had an epithelium—of ectodermic origin—with a thin intima cuticular.

At the base of the right lateral oviduct, near the place where the common oviduct begins, an oocyte approximately 0.25 mm in diameter was present; in this same cavity were the remains of the vitellus. The oocyte was immature and was completely surrounded by a thick layer of follicular cells that had begun to degenerate (Fig. 2G). Furthermore, in the anterior region of the common oviduct a second oocyte was found that measured approximately 0.70 mm in length, and a large amount of vitellus was spread throughout the cavity. This oocyte was also immature and was partially surrounded by follicular cells that were degenerating visibly (Fig. 2H). The vagina, spermatheca and spermathecal gland were similar to those of all females of this species.

As to the behavior of this female, by the time of dissection she had made a nest with four nest balls (equal to four eggs laid). She was beginning to make the second nest, which contained two nest balls, and she was making the third ball to lay another egg.

These observations, both anatomical and behavioral, show that the two ovaries and oviducts were functional. We cannot, however, insure that the eggs laid came from both ovaries. The fact that we found immature oocytes in the right oviduct indicates that vitellogenesis took place in the right ovary just as in the left, although this process may not have occurred simultaneously in both ovaries. It is possible, on the other hand, that the left ovary's signal to ovulate also activated the right ovary, causing the still immature oocytes to enter the oviduct, where they remained and began to degenerate.

Discussion

The *Canthon cyanellus cyanellus* female studied is an exceptional case. Over the past 13 years, we have maintained broods of this species for different research projects; therefore, we have records for the dissection of about 1000 females of known age and behavior, as well as information for females collected from the field. Furthermore, we have dissected between 10 and 15 females from each of 30 other species from different Scarabaeinae tribes. Until now, however, we had not found a single female with a reproductive system different from that of the standard female of this subfamily.

The *Canthon cyanellus cyanellus* female studied had not only two ovaries with one ovariole each but two lateral oviducts as well. Both the gonads and ducts were functional, and the female had oviposited several times. In the *Scarabeus sacer* female that Heymons studied in 1930, the second rudimentary ovariole of the left ovary had atrophied and its cells were degenerating. In 1979, Pluot observed that a *Onthophagus lecontei* female had a left ovary with two ovarioles of different sizes. The smaller ovariole was not functional and contained no oocytes and prefollicular cells; there was

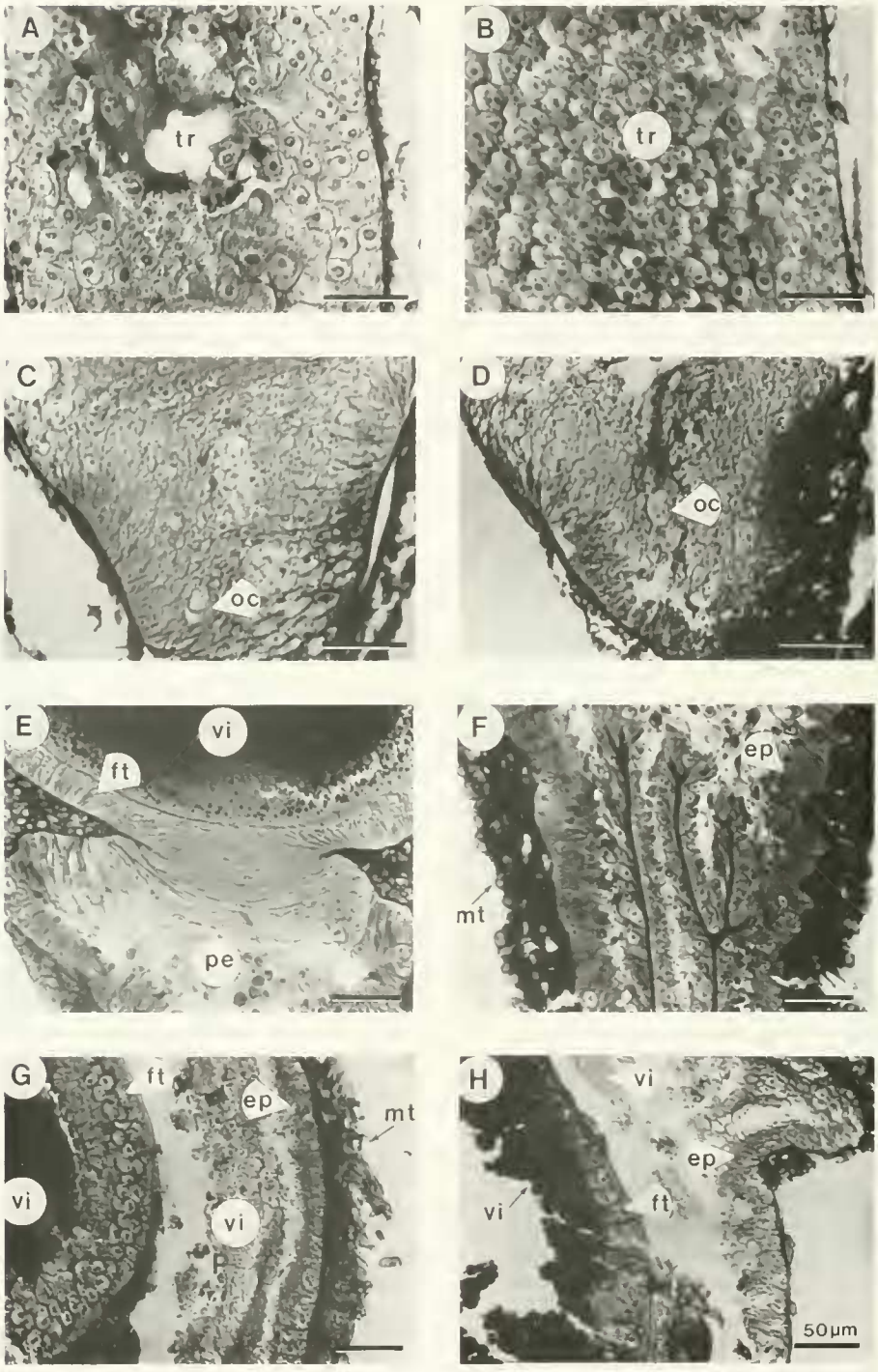

Fig. 2. Microphotographs of longitudinal histological cuts of the abnormal *Canthon cyanellus cyanellus* female reproductive system. A, Middle region of the germarium of the left ovary. B, Middle regions of the germarium of the right ovary. C, Basal region of the germarium of the left ovary. D, Basal region of the germarium of the right ovary. E, Basal oocyte of the right ovary and its pedicel. F, Anterior region of the right lateral oviduct. G, Posterior region of the right lateral oviduct. H, Anterior region of the common oviduct. Abbreviations: ep = epithelium of the oviduct; ft = follicular tissue; mt = muscular tissue; oc = oocyte surrounded by prefollicular tissue; pe = pedicel; tr = trophocytes; vi = vitellus.

no communication between the pedicel and germarium.

During ovarian organogenesis, at the end of larval development, the left ovarian rudiment of *Canthon indigaceus chevrolati* Harold and *Onthophagus* sp. had 6 ovarioles, 5 of which had atrophied. The right ovarian rudiment only contained 5 to 6 cellular masses which constituted the remains of the ovarioles. At the end of pupal development, the right ovarian rudiment, right lateral oviduct and 5 ovarioles of the left ovarian rudiment had degenerated (Pluot 1979).

According to Ritcher and Baker (1974), the basic number of Scarabaeoidea ovarioles seems to be 6 for each of the two ovaries (6-6). This characteristic appears without exception in Ochodaeinae, Geotrupinae, Acanthocerinae, and Melolonthinae and is also common in some species of Dynastinae, Rutelinae, Cetoniinae, Troginae, and Aphodiinae. In Scarabaeinae only 1-0 exists.

Taking into account the phylogenetic relationships between the different groups of Scarabaeoidea (Zunino 1983, D'Hotman and Scholtz 1990, Browne 1993) and the anatomic studies from the ovary of this group (Robertson 1961, Ritcher and Baker 1974), it can suppose that the reduction process at the ovariole nivel has an ancient origin since a phylogenetic point of view, and it can be attributed to subfamily common ancestor.

This reduction process could be unchained as of 6-6 (two ovaries with six ovarioles each one) to reach 1-0 (one ovary with only one ovariole) including not only the right ovary atrophy but the right lateral oviduct atrophy as well. It is also supported by an ontogenetic point of view. Observations done on *Canthon indigaceus chevrolati* and *Onthophagus* sp. regarding the atrophy of an ovary and five ovarioles from the other ovary during postembryonic development (Pluot 1979) provide such evidence, as does the fact that during early embryonic development in *Canthon, cyanellus cyanellus,* there are two similar ovarian rudiments with a 6-6 number of ovarioles (Martínez, unpublished data). The existence of adult females from other species in which the remains of ovarioles from the left ovary are observed (Heymons 1930, Pluot 1979) provides further evidence, as do the two ovaries with an ovariole and two lateral oviducts in the case of the *Canthon cyanellus cyanellus* female.

Further research during organogenesis is needed in order to determine what factors have induced this process of extreme reduction in female gonads, a process which has been related to complex reproductive behavior. It is also important to determine the reasons why in certain cases the reduction is not complete in adult females.

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